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The latest middle Eocene Primate Fauna in Pondaung area, Myanmar

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Abstract

So far four primate taxa have been discovered from the latest middle Eocene Pondaung Formation, Central Myanmar (= Burma): *Pondaungia cotteri*, *Amphipithecus mogaungensis*, *Bahinia pondaungensis*, and an unnamed new taxon. Especially the phylogenetic positions of *Pondaungia* and *Amphipithecus* have been discussed by many researchers since their first discoveries in the early part of this century. Recent new specimens, including maxillary fragments, of *Pondaungia* and *Amphipithecus* may reveal their taxonomic status and phylogenetic position in the evolution of early anthropoids in East Asia.

Introduction

It was at the beginning of the 20th century that the first mammal fossils were reported from the Pondaung area, Central Myanmar. Numerous teeth and bone fragments of large mammals, such as anthracotheres, aminodontids, and brontotheres (= titanotheres), were collected by paleontologists (Pilgrim and Cotter, 1916). In 1914, moreover, the primate fossils were collected near Pangan Village by Dr. G. de P. Cotter of the Geological Survey of India, and were described by G. E. Pilgrim in 1927. He regarded that they belong to the same individual, and named it *Pondaungia cotteri*. Following these discoveries of fossil materials, Dr. Barnum Brown of the American Museum of Natural History, visited Burma to collect vertebrate fossils in 1923. Although theBrown's collection has not been studied many years even after his returning to the U.S., Colbert (1937, 1938) described several mammal fossils, including a new primate taxon, *Amphipithecus mogaungensis*. Both *Pondaungia* and *Amphipithecus* were regarded as higher primates, the Anthropoidea, by Pilgrim (1927) and Colbert (1937), respectively.

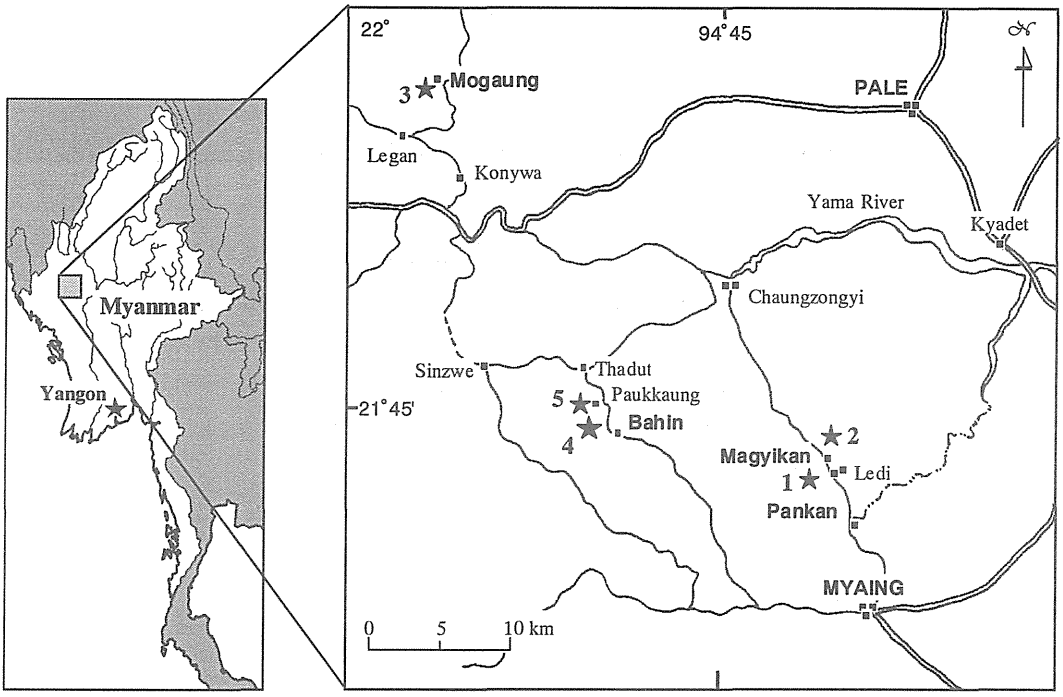

Figure 1. Index map of Myanmar and Pondaung area, showing several primate fossil localities. Star means primate fossil localities (1,type locality of *Pondaungia,* Pankan; 2, Taung Ni Gyin Kyitchaung, Pankan; Lema Kyitchaung, Mogaung; 4, Yarshe Kyitchaung, Bahin; 5, Paukkaung Kyitchaung, Bahin.

However, the phylogenetic position of these fossil primates were discussed by later students so many times: some researchers considered them as anthropoids (Simpson, 1945; Simons, 1963, 1965, 1971), some regarded them as adapoids or other primitive primates (Szalay, 1970, 1972; Szalay & Delson, 1979), and others identified them not primates but primitive mammals (von Koenigswald, 1965). This controversy has not yet been settled down because of the scanty of the fossil materials.

At the end of 1970s, several primate fossils were discovered at the Pondaung area again. Although these "second" specimens were identified as *Pondaungia* and *Amphipithecus* (Ba Maw *et al.*, 1979; Ciochon *et al.*, 1985), the controversy over their phylogenetic position were not established.

In the late 1990's, several paleontological investigations were carried out at the Pondaung area in order to find more primate specimens. These researches provided us new primate fossils including not only known *Pondaungia* and *Amphipithecus* but also two new primate taxa. In this paper we introduce the brief history of the discovery of primate fossils from the Pondaung area, and present several taxonomical and phylogenetic problems in the Pondaung primates.

Geological Setting

The Irrawaddy (= Ayeyarwady) River, which is one of the largest river in Myanmar,

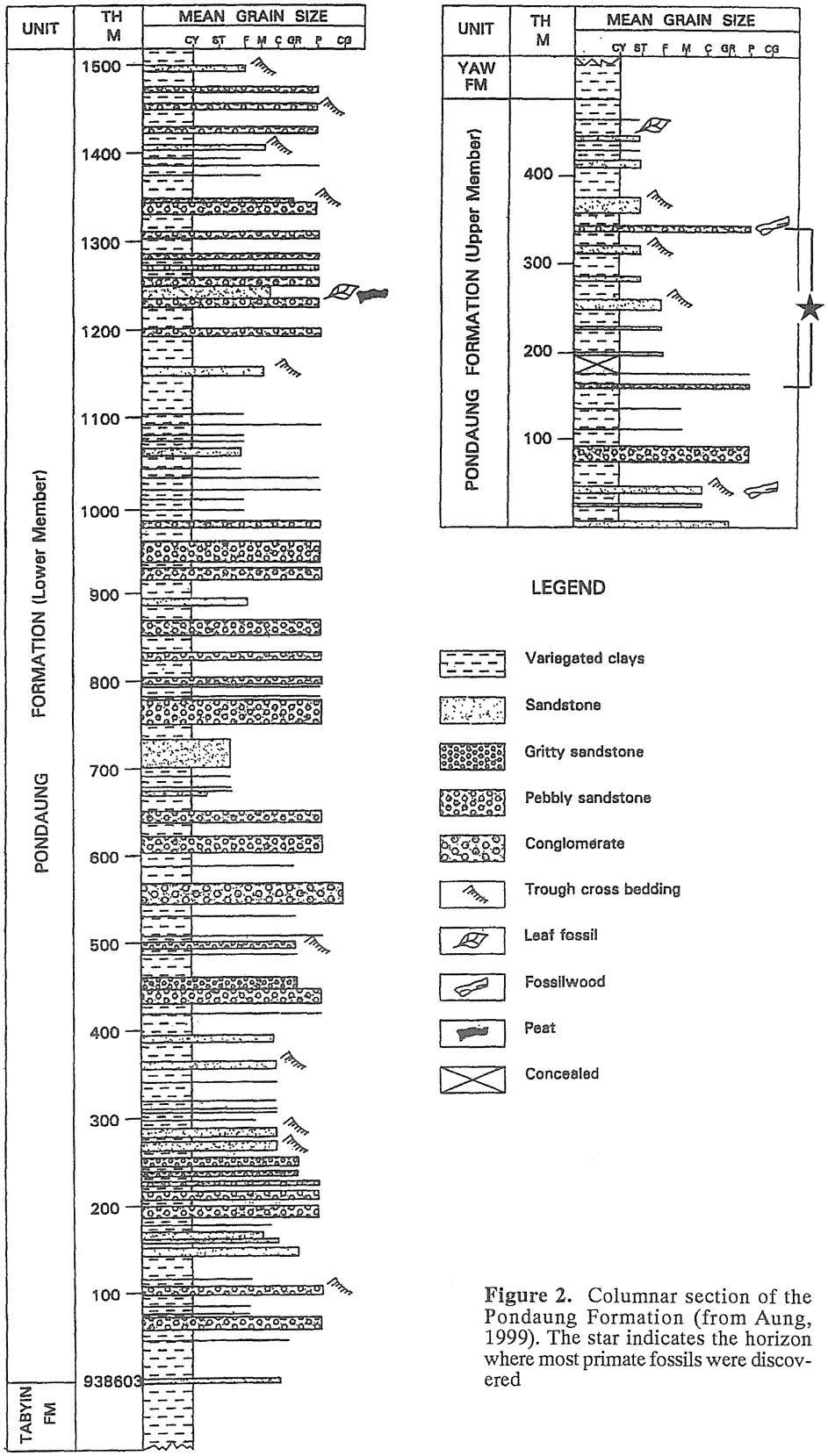

Figure 2. Columnar section of the Pondaung Formation (from Aung, 1999). The star indicates the horizon where most primate fossils were discovered

originates in the Tibetan plateau and flows southward through the Andaman Sea, penetrating the Central Lowlands of Myanmar. On the other hand, the Chindwin River, another big river in Myanmar, originates in the northern Myanmar and joins the Irrawaddy River at the Central Myanmar, about 50 km north of Pagan (= Bagan), the oldest capital. Along these Irrawaddy and Chindwin River, the Tertiary deposits are widely distributed and is called the Central Tertiary Belt (Colbert, 1938) or Inner Burman Tertiary Basin (Bender, 1983). This Central Tertiary Belt is bounded by the Shan Plateau on the east and by the folded Arakan Yoma (= mountain range) on the west.

In this Central Tertiary Belt there are several localities producing a rich mammal fossils: the Pondaung fauna of Upper Eocene age, the Lower Irrawaddy fauna of Pliocene age, and the Upper Irrawaddy fauna of Lower Pleistocene age. The mammal fossils of Pondaung Fauna have been mainly discovered from the Pondaung Formation (Pondaung Sandstone), which is underlain by the Tabyin Formation (Tabyin Clay) and overlain by the Yaw Formation (Yaw Shale) (Fig. 2). The Tabyin Formations is basically marine sediments and the Pondaung Formation, going upwards in the series, exhibits a gradual change from marine to brackish and finally to freshwater and land conditions. The marine Yaw Formation overlies the Pondaung Formation unconformably. From the south to the north the, on the other hand, the Pondaung Formation exhibits a progressive advance of continental sediments and a consequent retreat of marine deposition. It is generally believed that the continental sediments thicken gradually about 21°45'N to 23°30'N.

The Pondaung Formation is widely distributed between the Pondaung Hill Region in the west and the Chindwin River in the east, and can be divided into the Lower and Upper Members (Fig. 2, Aung, 1999; Aung Naing Soe, 1999). The Lower Member is about 1500 m in thick, consisting mainly of greenish pebbly sandstones and clays with some conglomerate, siltstones, and shale beds. The Upper Member is much thinner, about 500 m in thick, consisting mainly of fine- to medium-grain sandstone and variegated clay beds. Most of mammal fossils, including primate fossils, seem to have been collected from the Upper Members.

There are three main fossil localities at the Pondaung area, Pangan (= Pankan, Phangan)-Magyigan, Mogaung, and Bahin villages, all of which have produced primate fossils to date (Fig. 1). Although these localities are separated only 10-20 km from each other, it is very hard to move directly from one locality to the other because of a dense bush/scrub and of muddy passes in the hills. Stratigraphically, however, all these three localities are likely to correspond to the middle part of the Upper Member of the Pondaung Formation (Fig. 2, Aung, 1999; Aung Naing Soe, 1999). The exact geographical data of the fossil localities are explained by Tsubamoto *et al.* (in this volume).

The geological age of the Pondaung Formation was originally regarded as the late

Eocene age on the basis of the mammalian fossils, such as anthracotheres (artiodactyla), from the Pondaung Formation and of the marine invertebrate fossils, such as molluscs and foraminifers, from the overlying Yaw Formation (Pilgrim and Cotter, 1916). Later researchers, accepting their view, pointed out that the perissodactyls and artiodactyls of the Pondaung fauna are correlated to those of the Bartonian (or Ludian) Stage in Europe (Pilgrim, 1925, 1928). Colbert (1938) also indicated that the Pondaung fauna is correlated to the Uintan Land Mammal Age in North America and to the Shara Murun fauna in Inner Mongolia, both are considered as the late Eocene age.

Holroyd and Ciochon (1994), however, reviewed the geological age of the Pondaung fauna and concluded that it is the middle Eocene age on the basis of the following reasons: (1) the Shara Murun fauna is now regarded as the late middle Eocene, (2) recent studies of molluscs and microfossils (calcareous nannoplankton, planktonic foraminifera) indicate that the Pondaung fauna is correlated to the late Bartonian, which is now regarded as the late middle Eocene, (3) *Anthracokeryx* (a genus of anthracotheres), which is one of the most dominant mammals of the Pondaung fauna, is also reported from the latest middle Eocene sediments of Heti, northern China. Recently, moreover, Myanmar researchers also reported that the analysis of the nannofossils and pollens/spores of the Pondaung Formation suggests the NP-16 to NP-20 Nannoplankton Zone, which correspond to the middle to late Eocene age (Aung, 1999).

Brief History of Pondaung Primate Fossils

1. *Pondaungia*

First discovery of *Pondaungia* in 1910's

Pondaungia cotteri was first discovered from the Pondaung sandstone bed in Pangan Village in 1914, and was formally described in 1927. The holotype consists of three specimens, probably belonging to the same individual: a left maxillary fragment with M^{1-2} (GSI D 203), left mandibular fragment with M_{2-3} (GSI D 201), and right mandibular fragment with M_3 (GSI D 202). Pilgrim (1927) regarded *Pondaungia* as a primitive anthropoid, and many authorities agreed to his view (Colbert, 1938; Simpson, 1945; Simons, 1963, 1965, 1971). However, von Koenigswald (1965) considered *Pondaungia* not a primate but a primitive mammal, condylarthra. Szalay and Delson (1979) placed *Pondaungia* as incertae sedis in Infraorder Catarrhini.

The reason why the phylogenetic position of *Pondaungia* has not been agreed among researchers is that a distolingual cusp on the upper molars were differently identified by those researchers. The $M^{1,2}$ of *Pondaungia* are nearly rectangular in occlusal view with four main cusps: the paracone, protocone, metacone, and a small distolingual cusp, which seems to be connected with the protocone through a short ridge. There are three possibility

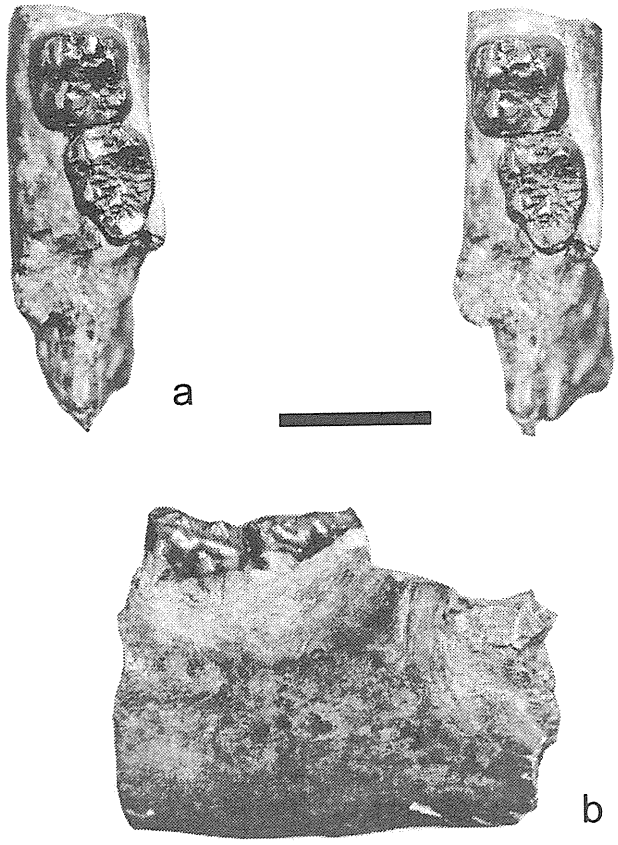

Figure 3. The second specimen of *P. cotteri*. Occlusal (a: stereo pair) and buccal (b) views of NMMP-3 (a left mandibular fragment with $M_{2,3}$). Scale bar = 1 cm.

in the identification of this cusp: a hypocone, pseudohypocone, or metaconule. It is generally believed that a true hypocone is originally derived from the (disto-) lingual cingulum and the connection between the protocone and hypocone is a secondary structure seen in later anthropoids. The presence of a true hypocone on upper molars has been regarded as one of the most critical character of anthropoid primates. If this cusp is a true hypocone, that is a positive character for the anthropoid status for *Pondaungia*. If this cusp is a pseudohypocone, *Pondaungia* is likely to be a prosimian. And although there has bee no student who regarded this cusp a metaconule so far, in this case *Pondaungia* would be regarded as a primitive mammal, such an artiodactyl.

Some researchers considered this cusp a true hypocone, and so *Pondaungia* should be an anthropoid (e.g. Pilgrim, 1927; Colbert, 1937). Other researchers insisted that this distolingual cusp is connected with a protoconid, so it should be a pseudohypocone, which has been splitted from the protocone. In the type specimen, GSI D202, although the distolingual cusp seems to be connected both with the distolingual and distal cingula, the occlusal surface of $M^{1,2}$ is somewhat eroded, making the idetification of this cusp difficult.

On the other hand, lower molars of the type specimen are also very eroded and show very few morphological information. M_2 is wider but slightly shorter than M_3. In M_2 the

trigonid is very slightly wider than the talonid, but its enamel surface is so badly eroded or broken that its detailed configuration is obscure. The presence/absence of the paraconid on lower molars, that is also one of the most definitive criteria for prosimians/anthropoids, cannot be confirmed unfortunately. In M_2 there is no distinct hypoconulid observed, while in M_3 the talonid tapers posteriorly. The buccal cingulid is very small or absent. It is interesting that an enamel crenulation is observed both in upper and lower molars.

Second specimens discovered in the late 1970's

More than sixty years after the discovery of the first specimen, the second specimens of *Pondaungia* were collected by Myanmar researchers at the Mogaung Village in April, 1978, where is the type locality of another fossil primate, *Amphipithecus mogaungensis*, (Fig. 1; Ba Maw *et al.*, 1979). This second specimen consists a right mandibular ramus with M_{2-3} (UCMP 120377, = DGMU-P1, NMMP 1). Although Ba Maw *et al.* (1979) described only this specimen, another mandibular specimen was collected in September of the same year. This specimen, a left mandibular ramus with M_{2-3} (DGMU-P2, = NMMP 3), looks very similar in overall shape and size to UCMP 12037. These second specimens are obviously larger than the type specimen both in dental and mandibular sizes (Table 3, Fig. 11), but were identified as the same species, *P. cotteri*. The mandibular rami of the second specimens are also very deep and robustly constructed compared with the type specimen.

Contrary to the poorly-preserved type specimen, however, the second specimens are in good condition to provide a detailed information of the dentition. In the M_2 trigonid there are three cusps present: the buccal one is obviously the protoconid but the identification of the lingual two is somewhat difficult. Although Ba Maw *et al.* (1979) identified these lingual two cusps as the paraconid and metaconid, there is another possibility that these cusps are the twin-peak of the metaconid, because they are too closely situated to each other to regard them as the different cusps and the preprotocrista runs anteriorly from the protoconid without connecting to the "paraconid".

As for the presence/absence of the hypoconulid in *Pondaungia*, there have been two opposing views: Ba Maw *et al.* (1979) reported the presence of the hypoconulid in a worn area on the M_2 of UCMP 120377, while Szalay and Delson (1979) denied the presence of this cusp. Even among the researchers who insist the presence of the hypoconulid, there seems no consensus of the position of the hypoconulid. Ciochon and Holroyd (1994) reexamined these second specimens and insist that the hypoconulid would have been present near the base of the hypoconid when the tooth was not worn.

Ciochon and Holroyd (1994) revised the phylogenetic position of *Pondaungia* as a notharctine adapid, enumerating following shared-derived features between *Pondaungia*

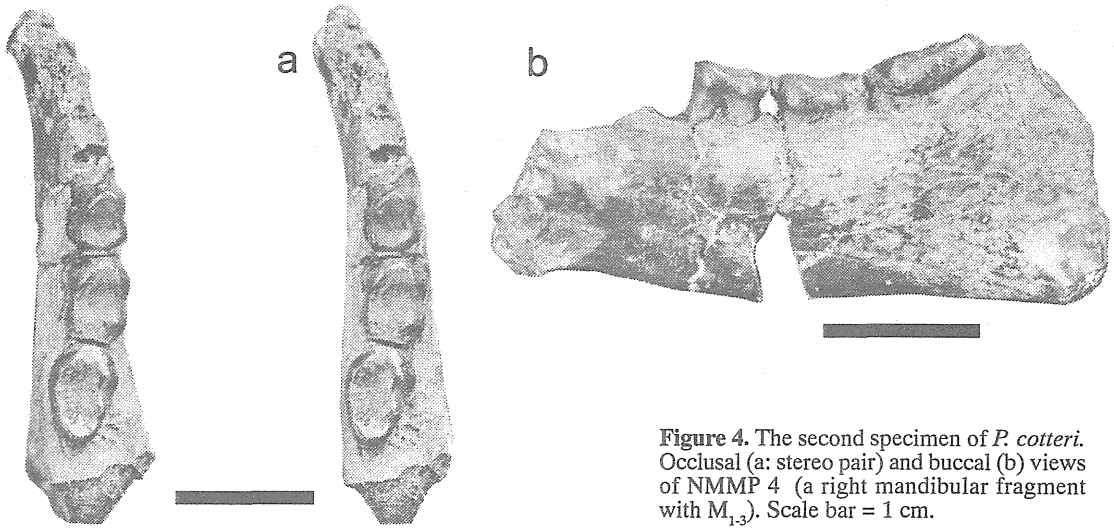

Figure 4. The second specimen of *P. cotteri*. Occlusal (a: stereo pair) and buccal (b) views of NMMP 4 (a right mandibular fragment with M_{1-3}). Scale bar = 1 cm.

and notharctines: (1) the paraconid is closely appressed to the metaconid and joined to the protoconid by mesially arcing paracristid. (2) a small M_2 hypoconulid is located at the distolingual base of the hypoconid. (3) the postprotocrista of upper molars is mesiodistally expanded to form a pseudohypocone. (4) the M_2 talonid is open posteriorly to form a confluent wear facet with trigonid basin of M_3 for occlusion of pseudohypocone. (5) the entoconids are relatively small. As already mentioned, however, most of these characters depend on the identifications of the distolingual cusp of upper molars, mesiolingual cusp of the M_2 trigonid, and the presence of the M_2 hypoconulid. The identification of the cusp relief on upper and lower molars would change the phyletic position of *Pondaungia* again.

Recent discoveries of *Pondaungia* in the late 1990's

In March and April of 1997, Myanmar researchers carried out a paleontological research at the Pondaung area, and discovered several primate specimens, two of which were identified as *Pondaungia*: NMMP 4 is a very shallow right mandibular fragment with poorly preserved M_{1-3} and alveola for $P_{3-4?}$, and NMMP 5 is a right mandibular fragment with M_{2-3} and posterior fragment of M_1. These two specimens were collected at the Lema Kyitchaung (= a small galley in Myanmar language) of the Mogaung village, where *Amphipithecus mogaungensis* (DGMU-P1) has been collected in 1978.

Jaeger *et al.* (1998) described NMMP 4 as a new species, *P. "minuta"*, on the basis of its much smaller size of teeth and mandible, and of the longer- and narrower-shaped $M_{1,2}$ than in *P. cotteri* (Table 3, Fig. 11). However, although NMMP 4 is actually significantly smaller than the second specimens, UCMP 120377 and DGPU-P2, it is not much smaller than the type specimen, GSI D201 and D203, in M_3 size. In NMMP 4, moreover, the enamel layer of lower molars is likely to be eroded or to have dropped down, making the

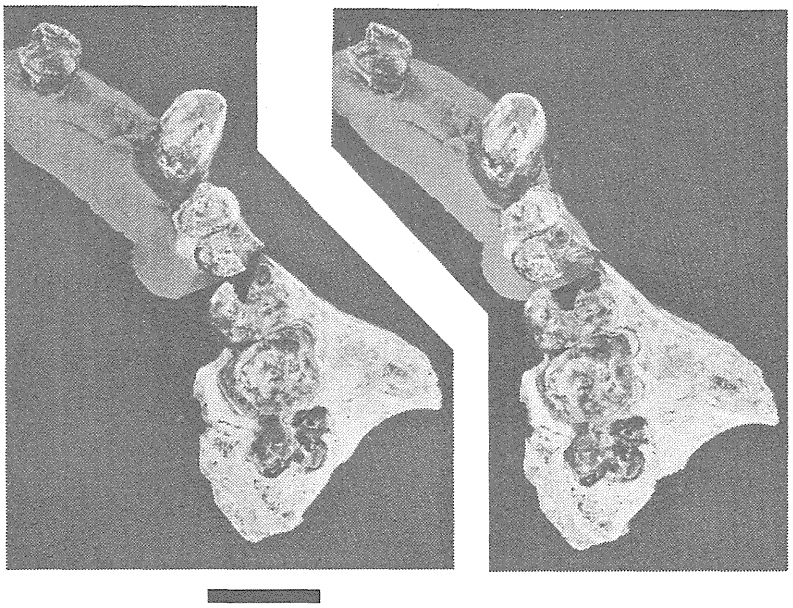

Figure 5. An occlusal view (stereo pair) of the new specimen of *Pondaungia cotteri*, NMMP-KU 0003: the left maxillary fragments with P^2, M^2, lingual parts of P^4 and M^1, a mesiolingual part of M^3, and isolated I^1 and C^1. Scale bar = 1 cm.

dental measurements of this specimen unreliable.

Despite being very worn and somewhat broken, on the other hand, NMMP 5 is very similar to those of UCMP 120377 and DGMU-P2 both in size and shape of the mandible and dentition. Therefore, among known specimens of *Pondaungia* there seems to be two groups: the smaller group including GSI-D 201, 203 and NMMP 4, and the larger one including UCMP 120377 and NMMP 3 and NMMP 5. This size-dimorphism in lower molars and mandible may reflect a sexual dimorphism in *Pondaungia* or a taxonomical confusion in Pondaung primates. It is necessary to review all the fossil specimens including not only *Pondaungia* but also another large primate, *Amphipithecus*.

In 1998 field season, moreover, the Myanmar-Japan joint expedition team discovered a new maxillary specimen with several upper teeth of *Pondaungia cotteri*, which consists of an isolated left I^1 and left C^1, left maxillary fragments with root of P^2, complete P^3, lingual halves of P^4 and M^1, complete M^2, and mesiolingual fragment of M^3 (NMMP-KU 0003). This specimen was collected at a new site, Taungni Kyitchaung of the Pangan village, and will be described by Shigehara *et al.* (in prep.) soon, so here we report briefly about this important materials.

The most striking find of this specimen is the maxillary fragment, which preserves the dorsal part of the zygomaticomaxillary bone and the root of the zygomatic arch. The maxillofacial part of this specimen suggests that *Pondaungia* has a rather broad and high face with the moderate size orbits, differing from the low face with large orbits of omomyoids. The dorsal part corresponds to the ventral surface of the orbit, a part of which

Table 1. Primate fossil specimens discovered from the Pondaung Forma

Specimen number	Taxonomic name	Description	Village	Kyitchaung	Discovery year	Expediton Team
GSI-D 201	*Pondaungia cotteri*	left mandible with M_{2-3}	Pangan	roadside	1914	
GSI-D 202	*Pondaungia cotteri*	left maxilla with M^{1-2}	Pangan	roadside	1914	
GSI-D 203	*Pondaungia cotteri*	right mandible with M_3	Pangan	roadside	1914	
AMNH 32520	*Amphipithecus mogaungensis*	left mandible with P_3-M_1	Mogaung	Thandaung?	1923	AMNH
UCMP 120377 (= DGMU-P4, NMMP 1)	*Pondaungia cotteri*	right mandible with M_{2-3}	Mogaung	Thandaung	1978	Myanmar
DGMU-P1 (= NMMP 2)	*Amphipithecus mogaungensis*	left mandible with M_{1-2}	Mogaung	Lema	1978	Myanmar
DGMU-P2 (= NMMP 3)	*Pondaungia cotteri*	left mandible with M_{2-3}	Mogaung	Thandaung	1978	Myanmar
NMMP 4	*Pondaungia "minuta"*	right mandible with M_{1-3} (infant?)	Mogaung	Lema	1997	Myanmar
NMMP 5	*Pondaungia cotteri*	right mandible with M_{2-3}	Mogaung	Lema	1997	Myanmar
NMMP 6	*Amphipithecus mogaungensis*	left mandible with M_{1-2}	Mogaung	Thandaung	1997	Myanmar
NMMP 7	*Amphipithecus "bahinensis"*	right mandibles with P_4-M_3 and left mandible with P_3-M_3	Bahin	Yarshe	1997	Myanmar
NMMP 15	*Bahinia pondaungensis*	right & left maxillae with C-M^2, & right mandible with P_2-l	Bahin	Yarshe	1998	Myanmar-France
NMMP 17	*Pondaungia cotteri*	right mandible with C-M_3	Mogaung	Thandaung	1998	Myanmr-France
NMMP-KU 0001	unnamed	right maxilla with P^4-M^3, left mandibles with C-P_3, and M_{2-}	Bahin	Yarshe	1998	Myanmar-Japan
NMMP-KU 0002	unnamed	left mandibe with M_3	Bahin	Yarshe	1998	Myanmar-Japan
NMMP-KU 0003	*Pondaungia cotteri*	left maxilla with I^1, C, P^3, (P^4-M^1), M^2, and (M^3)	Pangan	Taungni	1998	Myanmar-Japan
NMMP-KU 0004	*Pondaungia* ?	left female? upper canine	Pangan	Taungni	1998	Myanmar-Japan
NMMP-KU 0051	*Pondaungia cotteri*	buccal half of right M^1	Mogaung	Lema	1998	Myanmar-Japan
NMMP-KU 0115	primate or artiodactyla?	right femur	Bahin	Paukkaung	1998	Myanmar-Japan
NMMP-KU 0129	*Bahinia pondaungensis*	mandible with left C-M_1 and right I_2-C	Bahin	Yarshe	1998	Myanmar-Japan
NMMP-KU 0228	*Amphipithecus mogaungensis*	right maxilla with (P^4), M^{1-3}	Bahin	Paukkaung	1999	Myanmar-Japan
NMMP-KU 0229	*Amphipithecus mogaungensis*	parietal part of skull	Bahin	Paukkaung	1999	Myanmar-Japan

Table 2. Measurements of upper dentition of Pondaung primates.

		I^1		I^2		C^1		P^2		P^3	
Specimen No.	side	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
Pondaungia											
GSI D203*	L										
NMMP-KU 0003	L	(5.89)	4.52			7.70	6.40			3.58	5.53
Amphipithecus											
NMMP-KU 0228	R										

		P^4		M^1		M^2		M^3	
Specimen No.	side	MD	BL	MD	BL	MD	BL	MD	BL
Pondaungia									
GSI D203*	L			5.2	6.5	5.7	8.1		
NMMP-KU 0003	L	(3.85)	-	(5.83)	-	6.76	9.16	-	-
Amphipithecus									
NMMP-KU 0228	R			5.44	7.23	5.53	7.91	5.01	7.13

Data with* are adopted from Ba Maw *et al.* (1979) and with** are from Jaeger *et al.* (1998).
Measurements in parentheses are unreliable because of being badly damaged. R: right, L: left.

has been depressed during the fossilization, so the postorbital closure cannot be observed directly. However, the slight swelling of the ventral orbital surface of *Pondaungia* suggests, even if not complete, the partial postorbital closure of the sort seen in Aotus and Saimiri, both are platyrrhine monkeys.

Pondaungia has moderate sized $P^{3,4}$, and judging from the size of the root, P^2 is probably very small. Upper premolar are relatively small with respect to upper molars, so the snout is likely relatively short, differing from a long snout of adapoids.

The M^2 of NMMP-KU 0003 is far larger than that of the type specimen, GSI D 202, suggesting this new individual belong to the "larger group" of *Pondaungia*. In overall structure, therefore, *Pondaungia* differs from long-snouted adapoids/lemurs and from large-eyed omomyoids/tarsiers. *Pondaungia* seems to be a transitional form between the prosimians and anthropoids, showing a mosaic of primitive and derived morphological characters.

2. *Amphipithecus*

First discovery of *Amphipithecus* in 1920's

The type specimen of *Amphipithecus* was collected by Dr. Barnum Brown at the Mogaung village during a field research in 1923. However, it was not until Dr. E. Colbert of AMNH described this specimen in 1937, because the specimen was overlooked when it was catalogued within the museum collections (Colbert, 1937, 1938). The type specimen

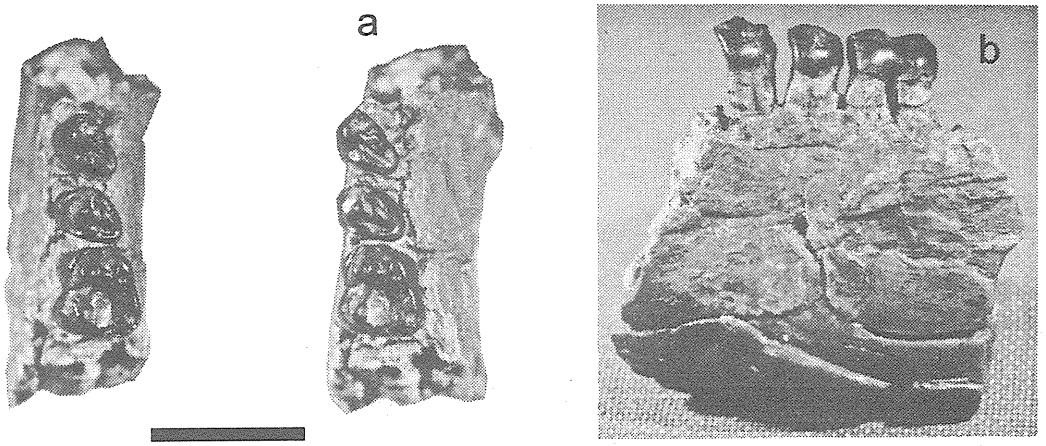

Figure 6. The second specimen of *Amphipithecus mogaungensis*. Occlusal (a: stereo pair) and buccal (b) views of AMNH 32520 (a left mandibular fragment with P_3-M_1). Scale bar = 1 cm.

consists of a left mandibular fragment with P_3-M_1 and roots of C_1 and P_2. The mandibular body is very deep relative to the size of lower dentition. The $P_{3,4}$ has a large protoconid and an indistinct metaconid. A small paraconid is present on P_3 but indistinct/absent on P_4. The P_4 is rather molariformed with a well developed talonid, while P_3 has only a shallow distolingual grove in place of the talonid. The occlusal outline of $P_{3,4}$ is described as "skewered" by Szalay (1970) or "teardrop" shaped by Ciochon and Holroyd (1994). On M_1 the trigonid is much narrower than the talonid, and a paraconid seems to be present on the center of the anterior end of the trigonid. Although Colbert (1937) described the possible existence of the hypoconulid at the talonid rim, it is very hard to recognize such structure on M_1 of the type specimen. P_3-M_1 has a very shallow buccal cingulid.

Colbert (1937) regarded *Amphipithecus* as an anthropoid primate on the basis of following dental and mandibular features: (1) the deep mandibular ramus, (2) the developed lingual (inferior?) transverse torus and the genioglossal pit at the symphysial region, (3) a rather posteriorly located mental foramen, and (4) an abbreviated vertical symphysis and upright canine. Simons (1963, 1965, 1971), supporting his view, pointed out the similarity between *Amphipithecus* and some anthropoid taxa, such as *Oligopithecus* and *Aegyptopithecus*, from the early Oligocene Fayum deposit, Egypt, and considered *Amphipithecus*, together with *Pondaungia*, as the earliest catarrhine monkeys. Szalay (1970) and Szalay and Delson (1979), however, insisted the adapid affinity of *Amphipithecus*, denying the close relationship with Fayum anthropoids on the basis of the following reasons: (1) the presence of a paraconid on M_1, (2) the large size and the shape of the M_1 talonid, (3) a rather buccally positioned hypoconulid on M_1 (he identified the presence of the hypoconulid on M_1 of the type specimen), and (4) the morphology of the P_3 and P_4. Gingerich (1980) also supported this adapoid hypothesis. This controversy was not settled because the fossil materials of *Amphipithecus* were too scanty to identify its phylogenetic

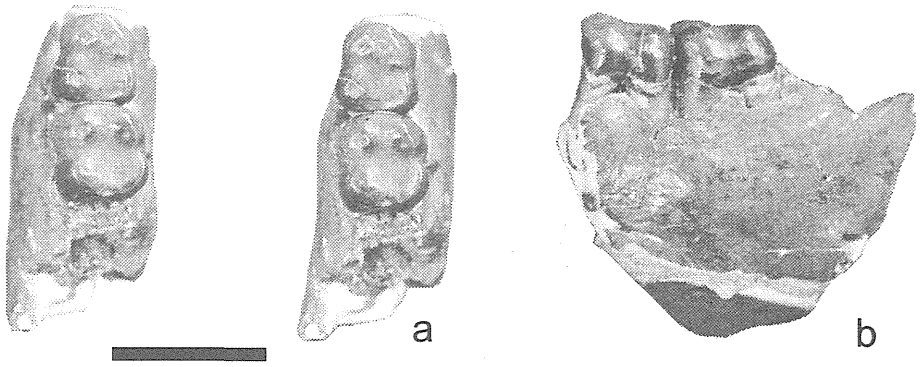

Figure 7. The second specimen of *A. mogaungensis.* Occlusal (a: stereo pair) and buccal (b) views of DGMU-P1 (a left mandibular fragment with $M_{1,2}$). Scale bar = 1 cm.

position.

Second specimens in the late 1970's

At the end of 1970's the second specimen of *Amphipithecus* was discovered by Myanmar researchers together with the new specimen of *Pondaungia*. This specimen, DGMU-P1 (= NMMP 2), consisting of a left mandibular fragment with M_{1-2}, was collected at the Lema Kyitchaung, Mogaung village, in 1978, and described later by Ciochon et al (1985).

As in the type specimen, M_1 of DGMU-P1 has a much narrower and longer trigonid than the talonid, while M_2 has a quadrate occlusal outline, with the trigonid and talonid nearly equal in height and buccolingual width. Moreover, although M_1 has a paraconid-like structure at the anterior end of the trigonid, M_2 has no paraconid. In DGMU-P1 there seems to be no sign of the hypoconulid both on M_1 and M_2, though Colbert (1937) mentions the presence of an "incipient" hypoconulid in the type specimen.

Although Ciochon et al (1985) regarded *Amphipithecus* as an anthropoid primate mainly on the basis of the morphology of M_2 of DGMU-P1, Ciochon and his coworkers, changing their morphological identification of the paraconid and hypoconulid, concluded that the phyletic position of *Amphipithecus* is obscure (Ciochon and Holroyd, 1994). Ciochon *et al.* (1985) originally described that there is no paraconid on M_2 of DGMU-P1, Ciochon and Holroyd (1994) say that "there is a slight centrally located bulge present on the anterior face of the trigonid" on M_2 of DGMU-P1. Ciochon and Holroyd (1994) also recognize the presence of the hypoconulid on lower molars of *Amphipithecus*, concurring with views of Szalay (1970, 1972) and Szalay and Delson (1979). They explain that as in some adapids the hypoconulid of *Amphipithecus* tend to disappear completely, leaving no

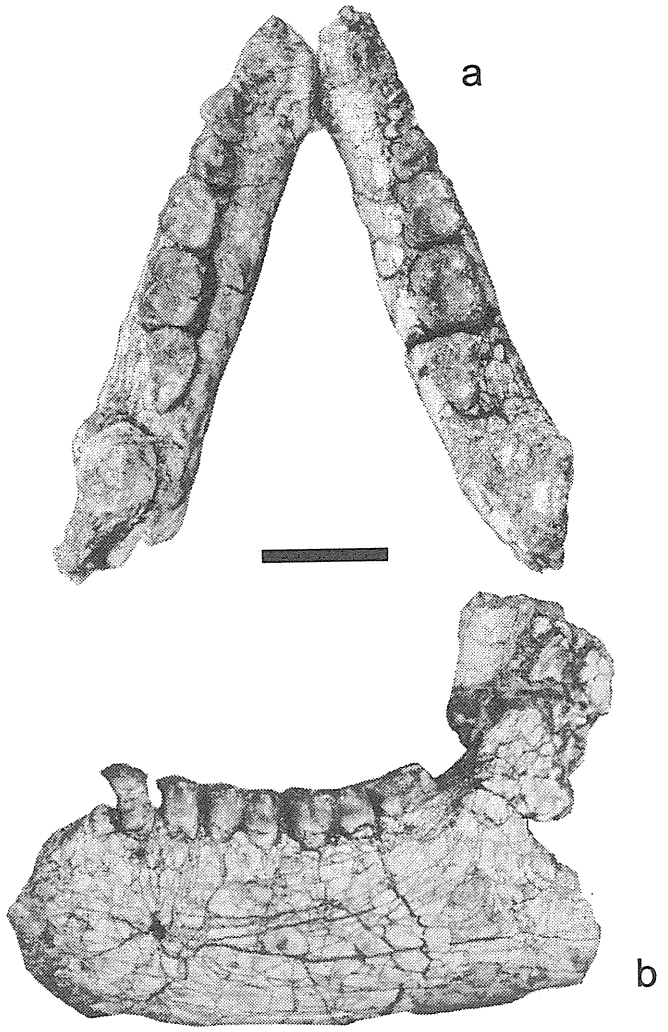

Figure 8. Photographs of *Amphipithecus "bahinensis"* (NMMP 7). The occlusal (a) and the buccal (b) views of the mandible. Scale bar = 1 cm.

trace of a dentine pit or any other evidence of its occurrence as the molar becomes worn. In this paper, however, they only showed the possibility of the presence of the hypoconulid on the worn molars of *Amphipithecus*, but did not prove the presence of the hypoconulid.

Recent discoveries of *Amphipithecus* in the late 1990's

As already mentioned, Myanmar researchers carried out the paleontological investigation at the Pondaung area in March-April of 1997, and discovered many mammal fossils, including a new specimens of *Amphipithecus*: NMMP 6 is a left mandibular fragment with $M_{1\text{-}2}$, and NMMP 7 consists of nearly complete right and left mandibles with right P_4-M_3 and left P_3-M_1. In the research report of the expedition NMMP 6 was identified as *A. mogaungensis*, while NMMP 7 was named as a new species, *A. "bahinensis"* (Pondaung Fossil Expedition Team, 1997). However, there is no significant morphological difference between *A. mogaungensis* and *A. "bahinensis"*. Jaeger *et al.* (1998) also regarded this specimen, NMMP 7, as *Amphipithecus mogaungensis* on the basis of the morphological

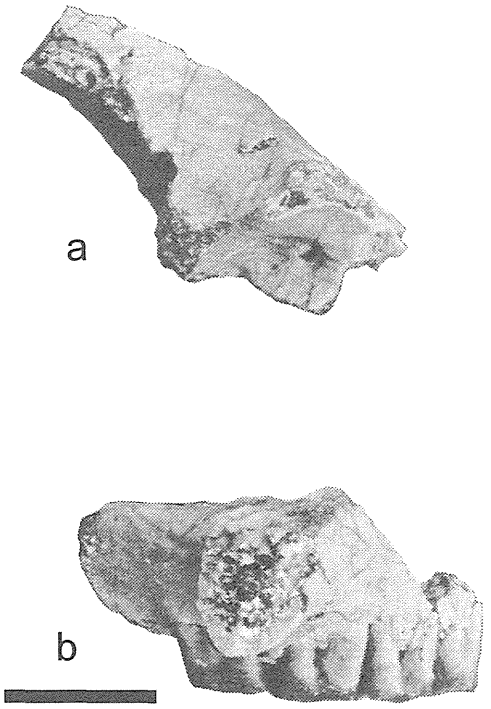

Figure 9. The newest specimen of *A. mogaungensis* (NMMP-KU 0228). Right lateral views of a parietal fragment (a) and maxillary fragment with M^{1-3} and posterior part of P^4 (b) . Scale bar = 1 cm.

similarities between AMNH 32520, DGMU-P1, and NMMP 7. In this paper we also agree their view that these specimens belong to the single taxon, *A. mogaungensis*.

NMMP 7, a pair of nearly complete mandibles, provide us many important characters of *A. mogaungensis*: The mandibular symphysis is rather vertical, and at the lingual face of the symphysis there are superior and inferior transverse tori and well developed genioglossal pit between them. The mandibular arcade is rather V-shaped, and the symphysis is not fused. The occlusal section of canine root suggests that this tooth is very compressed bilaterally and implanted diagonally to the cheek tooth row without forming the tooth-comb which is a shared-derived feature of extant prosimians. Judging from the size of the root, the P_2 is relatively small with respect to $P_{3,4}$. In M_1 the paraconid seems to be present at the mesial end of the trigonid, that is on the center line of the tooth. The M_2 seems to have neither paraconid nor hypoconulid. The M_3 is much smaller, both in mesio-distal and buccolingual dimension, than M_2.

3. *Bahinia*

Bahinia pondaungensis was first discovered at the Yashe Kyitchaung , Bahin Village, in 1998 (Jaeger *et al.*, 1999). The type specimen consists of a right maxillofacial fragment with C^1-M^2 (NMMP 15) and a left maxillary fragment with C^1-M^3 (NMMP 14) and a right mandibular fragment with P_2, P_4-M_1 (NMMP 16). Jaeger *et al.* (1999) interpreted this animal as a new representative of the family Eosimiidae, which has been discovered from

Table 3-2. Dental measurements of lower dentition of *Pondaungia* and *Amphipithecus*.

		C_1		P_2		P_3		P_4	
Specimen No.	side	max	min	MD	BL	MD	BL	MD	BL
Pondaungia									
UCMP 120377*	R								
GSI D201**	L								
GSI D202**	R								
DGMU-P2**	L								
NMMP 5**	R								
NMMP 4 **	R								
Amphipithecus									
AMNH 32520**	L					4.2	4.3	4.7	4.4
DGMU-P1**	L								
NMMP 6**	L								
NMMP 7**	L					4.5	3.7	4.4	4.1
NMMP 7**	R							4.5	3.8

Data with* are adopted from Ba Maw *et al.* (1979) and with** are from Jaeger *et al.* (1998). R: right, L: left.

the Middle Eocene deposits of China (Beard *et al.*, 1994, 1996; Tong, 1997). Among three premolars of *Bahinia*, the second premolar is much smaller than others. The $M^{1,2}$ are tricuped with a nearly complete buccal and lingual cingulum, and Jaeger *et al.* (1999) report a "very slight hypocone swelling on M^1 and M^2". The P_4 has a well developed talonid but no metaconid. The M_1 has a distinct paraconid and "buccodistally projecting hypoconulid" (Jaeger *et al.*, 1999).

It is very interesting that an anterior part of the mandibular specimen (NMMP 16) of the holotype was discovered independently by Myanmar-Japan Expedition Team. This specimen, NMMP-KU 0129, consists of a left mandibular fragment with C_1, $P_{2\text{-}4}$, trigonid of M_1, and root of I_2 and a anterior part of the right mandible with I_1 and parts of I_2 and C_1. NMMP 16 and NMMP-KU 0129 were collected at the same spot, and coincide each other. Unfortunately, it is hard to observe whether the mandibular symphysis is fused or not, because the mandibular arcade is broken at the symphysial part. The lower incisors are implanted vertically and not as procumbent as in extant prosimians. Compared with *Eosimias* from China (Beard *et al.*, 1994, 1996; Tong, 1997), *Bahinia* has a much deeper and more robust mandible.

Despite the presence of the paraconid on $M_{1,2}$ and the substantial absence of the hypocone on $M^{1,2}$, Jaeger *et al.* (1999) regarded *Bahinia* as an anthropoid primate, because the Eosimiidae is now regarded as one of the most primitive anthropoid by many

Table 3 -2.. Dental measurements of lower dentition of *Pondaungia* and *Amphipithecus*.

		M_1			M_2			M_3	
Specimen No.	side	MD	trdBL	tadBL	MD	trdBL	tadBL	MD	BL
Pondaungia									
UCMP 120377*	R				7.1	6.8	6.7	8.3	6.0
GSI D201**	L				6.6	5.6	5.3	7.3	4.7
GSI D202**	R							7.2	4.9
DGMU-P2**	L				7.0	6.8	6.8	8.5	6.1
NMMP 5**	R				7.3	6.7	(6.2)	8.7	6.0
NMMP 4 **	R	(5.6)	(3.4)	(4.0)	(6.6)	(4.7)	(4.8)	7.6	5.2
Amphipithecus									
AMNH 32520**	L	6.1	5.0	5.8					
DGMU-P1**	L	6.3	5.2	5.5	6.9	6.1	6.0		
NMMP 6**	L	6.3	5.3	5.5	6.8	6.0	6.1		
NMMP 7**	L	6.5	4.8	5.4	6.8	5.7	5.9	6.1	5.0
NMMP 7**	R	6.2	4.7	5.3	7.0	5.6	5.8	6.2	5.5

Measurements in parentheses are unreliable because of being badly damaged

researchers (Beard *et al.*, 1994, 1996; Tong, 1997; Kay *et al.*, 1997; Ross *et al.*, 1998). The presence of the Eosimiidae in the latest middle Eocene age in Myanmar suggest a vast distribution not only of this family but also of anthropoids during the middle to late Eocene in East Asia.

4. Unnamed specimen

During the 1998 field season, another new fossil primate was discovered at the Yashe Kyitchaung, Bahin Village, where *A. "bahinensis"* (NMMP 7) and *Bahinia* were collected. The specimens consist of the right maxillary fragments with P^4-M^3 and left mandibular fragments with C_1-P_3 and $M_{2\text{-}3}$ (NMMP-KU 0001, Fig. 10) and a left mandibular fragment with M_3 (NMMP-KU 0002). This new primate is slightly larger than *Bahinia* and much smaller than *Amphipithecus* and *Pondaungia*. Upper molars have a square occlusal outline with four cusps. $M_{2,3}$ has a very short trigonid and enamel crenulation is observed. This specimen will be described soon (Takai *et al.*, in prep).

Generic differentiation between *Pondaungia* and *Amphipithecus*

From the latest middle Eocene sediments of the Pondaung area, four primate taxa have been discovered so far: *Pondaungia cotteri*, *Amphipithecus mogaungensis*, *Bahinia pondaungensis*, and an unnamed new genus (NMMP-KU 0001, 0002). Although recently two new species, *P. "minuta"* and *A. "bahinensis"*, were proposed French and Myanmar

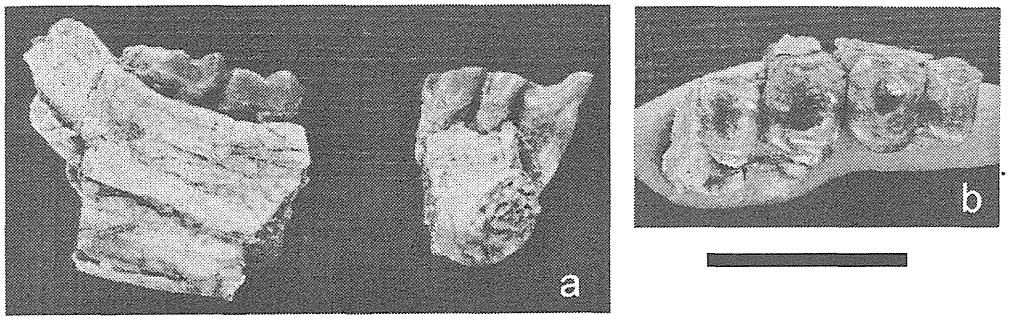

Figure 10. An unnamed new primate (NMMP-KU 0001). a: lingual view of the left mandibular fragments. b: occlusal view of right P^4-M^3.

researchers (Jaeger *et al.*, 1998; Pondaung Expedition Team, 1997), these two seem to be the junior synonym of *P. cotteri* and *A. mogaungensis*, respectively. As for *P. "minuta"*, NMMP 4 actually has a very shallow mandibular manus with relatively small lower molars, but its M_3 is not smaller but slightly larger than that the type specimen (GSI D201, 203) of *P. cotteri* (Fig. 11).

However, on the other hand, NMMP 4 is obviously smaller than several specimens of *P. cotteri* (UCMP 120377, DGMU-P2. NMMP 5) in the size of $M_{2,3}$ (Table 3, Fig. 11). This size-dimorphism seen in *Pondaungia* can be interpreted by two alternative hypotheses: an extreme sexual dimorphism in *P. cotteri* or an interspecific variation within the genus *Pondaungia.* In this paper we cannot decide which hypothesis is more probable than the other, owing to the scanty of fossil materials. Judging from the dental and mandibular size, it is not strange that *Pondaungia* has a large sexual dimorphism in the dentition and mandible, but *Amphipithecus,* a nearly same-sized sympatric primate, does not show any dimorphism among the present fossil specimens. At present, therefore, we can only say that the "larger-size group" of *Pondaungia* (including UCMP 120377, DGMU-P2, NMMP 5, and NMMP-KU 0003) might be representative for another species of *Pondaungia*.

Another remaining taxonomic problem of Pondaung primates is a generic differentiation between *Pondaungia* and *Amphipithecus*. *Pondaungia* was first described in 1927 on the basis of the $M^{1\text{-}2}$ and $M_{2\text{-}3}$. Although the upper and lower dentition were somewhat eroded, basic morphological information were obtained. When Colbert (1937) established *Amphipithecus* on the basis of P_3-M_1, he described that *Pondaungia* has a shallower mandibular, more square-outlined lower molars, and more transversely aligned lower molar cusps with respect to *Amphipithecus*. However, this definition of *Amphipithecus* is based on the observation not of $M_{2,3}$ but of P_3-M_1. Later specimens of *Amphipithecus* revealed that this diagnosis does not apply to M_2 of *Amphipithecus*, which has very square occlusal

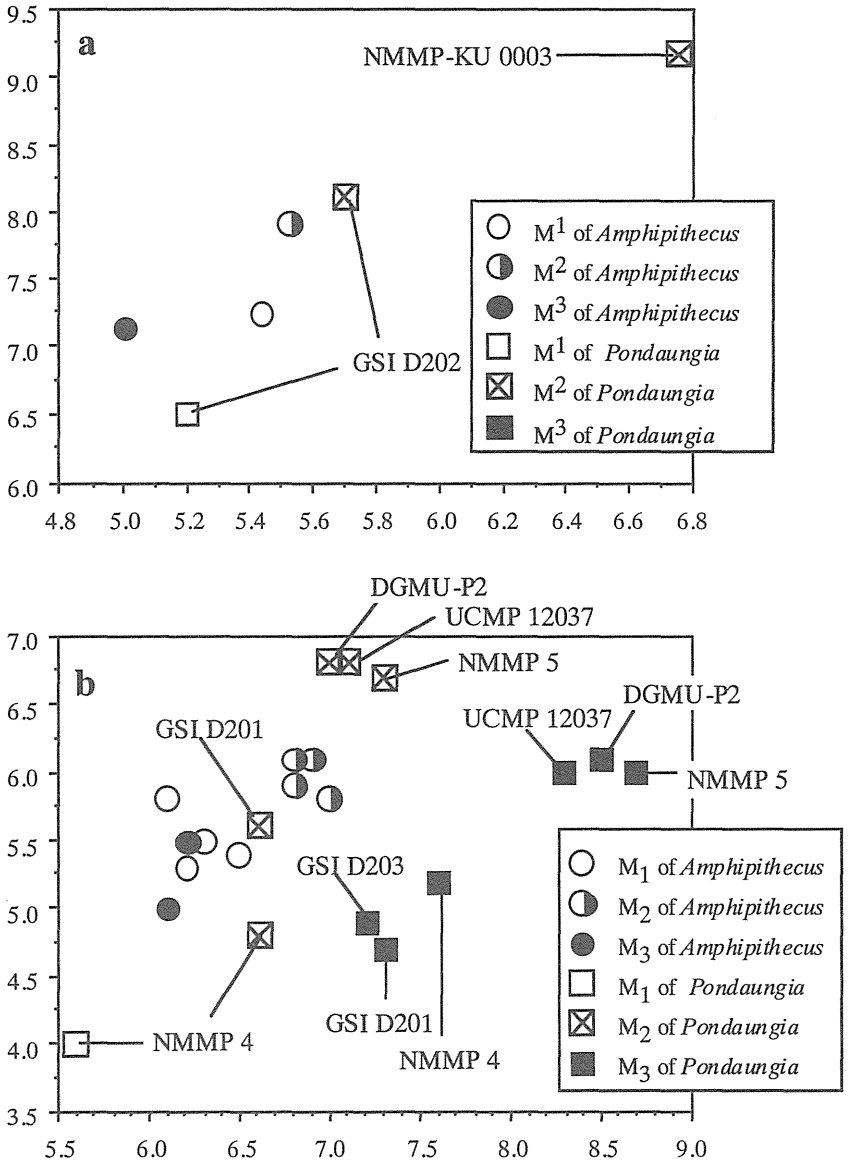

Figure 11. Scatterplots of the upper (a) and lower (b) molars of *Pondaungia* and *Amphipithecus*. MD: mesiodistal length (mm). BL: buccolingual width (mm). Note that the size-dimorphism seen on M2, 3 of *Pondaungia*.

outline with transversely aligned cusps. Moreover, lower molars of *Amphipithecus* seem to have a tendency to be worn rapidly and it is hard to observe the detailed configuration of the occlusal surface of the teeth.

At present, therefore, the only definitive difference between *Amphipithecus* and *Pondaungia* is the relative size of M_2 and M_3. In *Amphipithecus* M_3 is smaller than M_2 both in buccolingual width and mesiodistal length, while in *Pondaungia* (including both the "large" and "small" groups) M_3 is obviously longer and slightly narrower than M_2 (Fig. 11). The newest maxillary specimen, NMMP-KU 0228, of *Amphipithecus* also keeps this rule in upper molar dimension.

In the shape of the dental arcade, on the other hand, the mandibular arcade of *Amphipithecus* (NMMP 7) is rather V-shaped with a relatively acute angle of the symphysis (FIg. 8a), while in *Pondaungia* the upper premolars are relatively small and I^1 and upper molars are relatively large (NMMP-KU 0003, FIg. 5), suggesting that the face of *Pondaungia* is rather short and its dental arcade is less V-shaped, more parabolic in occlusal view than in *Amphipithecus*.

Jaeger *et al.* (1998) insist that *Pondaungia* and *Amphipithecus* belong to a single monophyletic group, the Amphipithecidae, together with *Siamopithecus*, which is discovered from the latest Eocene of Krabi, southern Thailand (Chaimanee *et al.*, 1997; Ducrocq, 1998, 1999). They define this family by the following characters: (1) the lower jaw is very deep, (2) lower molars are bunodont with low and very inflated cusps, (3) the paraconid and hypoconulid are very reduced/absent, (4) the labial cingulid are reduced/absent, (5) the trigonid and talonid of M^1 are of similar height, (6) M_2 is waisted, (7) M_3 is reduced with respect to M_2, (8) molar enamel surface is crenulated, and (9) upper molars has a distinct crest linking the hypocone and protocone. All these characters but the relative size of M_2 and M_3 hold true to *Pondaungia* and *Amphipithecus*: both in *Pondaungia* and *Siamopithecus* M_3 is not reduced but much longer than M_2, so the M_3 reduction is observed only in *Amphipithecus*.

Certainly, *Siamopithecus* and Pondaungia are very similar to each other in lower molars and mandibular ramus, but in upper dentition, especially in upper premolars, they are very different from each other: in *Siamopithecus* $P^{3,4}$ have a pear-like occlusal outline with a much larger paracone than protocone, while in *Pondaungia* $P^{3,4}$ have an oval outline with equal-sized, low paracone and protocone. At present we don't know which character, that is morphological similarity in lower molars and mandible or difference in upper premolars, we have to take seriously. More fossil remains will resolve this taxonomic problem in Pondaung primates.

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